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The assimilation number and its variations in the cultures and natural populations of marine phytoplankton

by V.I. Vedernikov

Chorophyll "a" and other pigments as indicators of the photosynthetic activity of phytoplankton

Investigation of the pigment system of plants is of great importance when studying photosynthesis. Pigments are borne and synthesized in individual granular formations of the plant cell called plastids, which are found in all photosynthesizing organisms [Bazhanov et al., 1964].

The pigments of plastids encountered in marine phytoplankton can be classified into the following four large groups on the basis of their chemical structure: chlorophylls "a", "b" and "c", biliproteides (phycoerythrin and phycocyanin), carotenes and xanthophylls. The last two are often combined in the carotenoid group.

(93)

The qualitative distribution of pigments among the various taxonomic groups of marine phytoplankton has been studied by a number of researchers [Humphrey, 1962; Parsons, 1961; Strickland,

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1960, 1965; Bogorad, 1962; Finenko et al., 1971]. Chorophyll "a", carotenes and xanthophylls are found in all the groups of algae. Chlorophyll "c" is encountered in diatoms, peridinians, chrysomonads (silicoflagellates, coccoliths and chrysophytes) and cryptomonads. Chlorophyll "b" is characteristic only of green algae, while phycocyanin and phycoerythrin are characteristic of blue-green algae and cryptomonads.

The content of pigments in marine planktonic algae is not very high. Quantitative determinations of the pigment content in the cultures of various algae at the stage of logarithmic growth have shown that chlorophyll "a" constitutes 0.2-2.2% of the dry weight of the algae, and all the pigments combined 0.8-3.7% [Parsons, 1961; Parsons et al., 1961].

On the basis of the data of numerous authors [Jeffrey, 1961; Parsons, 1961; Humphrey, 1963; Jeffrey, Allen, 1964; Madgwick, 1966; Riley, Wilson, 1967; Finenko, Lanskaya, 1968], we calculated the mean chlorophyll ratios in various groups of algae which are characteristic of marine phytoplankton. The ratio of chlorophyll "b" to chlorophyll "a" in green algae was found to be equal to 0.43 ± 0.22. The ratio of chlorophyll "c" to chlorophyll "a" amounted to 0.62 ± 0.13 for diatoms, 0.86 ± 0.56 for peridinians, 0.58 ± 0.46 for chrysomonads, and 0.51 ± 0.24 for cryptomonads. The only determination of this ratio for the Heterocontae gave us 0.72. In the oceans, diatoms are usually the main component of the phytoplankton [Cushing, 1955]; therefore, chlorophyll "a" should be regarded as the most important pigment with respect to its quantitative content in the living cells of marine phytoplankton.

Chlorophyll "a" is also of primary importance in the process of photosynthesis in green plants and algae. On the basis of experimental data obtained mainly in studies of red and brown algae, photobiochemists believed for quite some time that chlorophyll "a" was the only pigment which directly took part in photosynthesis in all photosynthesizing organisms [Duysens, 1951; Rabinovich, 1953, and others]. The role of the other pigments, considered to be secondary ones, boiled down to the absorption of light energy and resonant transfer of it to chlorophyll "a".

At the same time, we have recently witnessed the development of ideas that the secondary pigments not only transfer all the absorbed light energy to chlorophyll "a", but can partly utilize it in independent photoreactions which under certain conditions are of great importance to the photosynthetic process as a whole [Duysens, 1964; Fujita, 1970; Heath, 1972, etc.]. It is assumed that the primary reactions of photosynthesis take place as a result of two photochemical reactions which occur in two pigment systems, i.e. a long-wave reaction induced by a distant red light $\lambda > 680$ nm, and a short-wave reaction induced by light $\lambda < 670$ nm. The first pigment system is made up of the long-wave forms of chlorophyll "a", and the second system is composed of the short-wave forms of chlorophyll "a" with absorption maxima of about 660-670 nm and of secondary pigments. Effective photosynthesis requires the cooperate action of both pigment systems, when each of them gets a sufficient number of photons of the corresponding wavelengths. In the case where activation occurs in only one of the systems, the quantum efficiency of photosynthesis should diminish.

(94)

When studying the relationship between the quantity of plastid pigments and the intensity of photosynthesis during optimal or near-optimal light intensities, we ask ourselves which pigments are better to use as an indicator of the photosynthetic activity of phytoplankton. It is difficult to solve this problem a priori. On the one hand, the introduction of chlorophylls "b" and "c" and carotenoids, in addition to chlorophyll "a", into the correlative analysis of the "pigment-production" relationship can increase the coefficient of correlation (r), inasmuch as the secondary pigments increase the effectiveness of photosynthesis [Rabinovich, 1959]. On the other hand, the higher rate of the physiological cycle of chlorophyll "a" [Ballester, 1966] and its lower resistance to decomposition [Yentsch, Ryther, 1959b; Jeffrey, Allen, 1964] as compared with the secondary pigments could make this pigment a more reliable indicator of the photosynthetic activity of phytoplankton.

Some authors support the first of these two assumptions. Referring to the unpublished results of his experiments, Currie [Currie, 1958] maintains that there is better agreement between the sum of all the pigments contained in marine phytoplankton and the intensity of photosynthesis, than between the latter and only chlorophyll "a". On the basis of experiments with freshwater phytoplankton, I.L. Pyrina [1967] also surmises that the intensity of photosynthesis of phytoplankton is more closely related to the content of total chlorophyll, than to chlorophyll "a". However, we should note that this author has demonstrated this difference only for 12 samples with a relatively high content of chlorophylls "b" and "c".

Contrary results were obtained by Anderson and Banse [1965] and Doty and Oguri [1959]. During one of the ten runs of the Brown Bear research vessel in Oregon coastal waters (43-48°N) [Anderson, Base, 1965], the production—chlorophyll "a" correlation coefficient was several times higher than the production—total chlorophyll correlation coefficient. During the other nine runs, the difference between these coefficients proved to be insignificant. During Doty and Oguri's investigations in Hawaiian coastal waters, the partial coefficient of production—chlorophyll "a" correlation was 2.5 times greater than the multiple coefficient of production—total plant pigment correlation, though the difference between these coefficients in the productive oceanic waters east of Australia also proved to be insignificant.

The results of our investigations in the southeastern part of the Pacific Ocean [Vedernikov, 1970; Vedernikov, Starodubtsev, 1971] are not at variance with these two studies. On the basis of 118 measurements [of differences - transl.] between production and the content of pigments in the surface layer by means of the least-squares method, we arrived at the following relationships:

$$\lg C_{\phi n} = 1.96 + 1.12 \lg C_a \ (r = +0.90),$$

$$\lg C_{\phi n} = 1.54 + 1.29 \lg C_\Sigma \ (r = +0.85),$$

where $C_{\phi n}$ denotes production in the surface layer in mg C/m^3 per day, C_a and C_Σ are the concentrations of chlorophyll "a" and the sums of chlorophylls "a", "b" and "c" in the surface layer in mg/m^3, and r is the coefficient of correlation between the logarithms of the values.

Though the coefficient of correlation for the first of the two relationships presented above is somewhat higher than for the second one, the difference between them is insignificant.

(95)

Thus, on the basis of our own investigations and the literature, we can say that the inclusion of carotenoids or other chlorophylls in addition to chlorophyll "a" in the statistical analysis of marine basins does not usually increase, and sometimes even reduces the coefficient of correlation between production and plant pigments. The results of Cassie's experiments [Cassie, 1963] with a bacteria-free culture of diatom algae Skeletonema costatum also show that chlorophyll "a" and carotenoids can in some cases weaken the relationship between the pigments and the intensity of photosynthesis. In these investigations, the partial coefficients of correlation between the intensity of photosynthesis and the secondary pigments were either positive or negative, depending on the light conditions in which the plant cells were found prior to and during the experiment.

Considering the experimental data presented above, as well as the inadequacy of the standard method of determining secondary pigments and their relatively high resistance to decomposition, we should say that only chlorophyll "a" should be regarded as the indicator of the photosynthetic activity of natural populations of marine phytoplankton in routine investigations. From this it follows that it is better to calculate the assimilation number (AN) only for chlorophyll "a", instead of for all the chlorophylls combined, or for all the pigments contained in marine phytoplankton.

DETERMINATION OF THE ASSIMILATION NUMBER

Many scientists have applied regression analysis to study the relationship between the content of chlorophyll "a" and production [Holmes et al., 1958; Rodhe et al., 1958; Anderson, Banse, 1965; El-Sayed, 1968; Vedernikov, Starodubtsev, 1971, etc.]. The use of regression equations for studying this type of relationship is not always convenient, as, first of all, this relationship can be either linear or curvilinear, and secondly, the value a in the equation $C_{\phi n} = a+bC_a$ can be either positive or negative in the case of a linear relationship. The assimilation number is a characteristic which facilitates the analysis of this relationship, inasmuch as AN values remain positive and usually vary within the limits of one order.

The term "assimilation number" was introduced by the German physiologists R. Willstätter and A. Stoll [1918]. According to their definition, the assimilation number is the maximum quantity of carbon dioxide which can be reduced per time unit by a unit of chlorophyll content in a cell or tissue under optimal conditions. In the contemporary literature devoted to the study of the ecology of phytoplankton photosynthesis, the assimilation number is regarded as the relationship between the intensity of photosynthesis and chlorophyll under various light intensities, and is frequently expressed in units of the carbon content fixed by a unit of chlorophyll content during a specific time interval [Strickland, 1960; Vinberg, 1960; Curl, Small, 1965; Burkholder, Burkholder, 1967; Finenko, 1967, 1970; Koblents-Mishke et al., 1970]. This time interval is usually one hour, and the values

associated with it will be referred to as simply assimilation numbers. G.G. Vinberg [1960] introduced the idea of a diurnal assimilation number (DAN). DAN is more convenient when applying 24-hour exposure of bottles in natural bodies of water; it is of both physiological and ecological significance, as it depends on the duration of daylight, which naturally varies throughout the year and at different latitudes. The analogue of the diurnal assimilation number is the daytime assimilation number (DTAN) which is more convenient to use when bottles are being exposed in natural light during half of the daylight hours. (96)

This paper discusses the natural fluctuations in the assimilation number, rather than the diurnal or daytime assimilation numbers, as it is easier to analyze the relationship between the assimilative activity of chlorophyll and environmental factors when the length of the daylight period does not have to be taken into account.

It is not difficult to calculate the values of assimilation numbers measured under the conditions of continuous artificial illumination. It is more difficult to estimate assimilation numbers when samples are exposed to natural light, usually during the first or second half of the daylight period. During Curl and Small's 2-hour in situ experiments [Curl, Small, 1965], the layer of optimal light conditions, which we consider as being the layer of the maximum assimilation number, either remained at the surface throughout the entire day, or moved from the surface in the morning to the deeper layers by midday, and then back again to the surface in the evening. Having analyzed these data, we attempted

to compare the results of these 2-hour experiments with the averaged assimilation number for a day at each of the studied levels. This averaged value corresponds roughly to the value of the assimilation number measured during standard determination of production. We found that the layer of the maximum AN obtained for a day during the 2-hour exposures coincided with the layer of the maximum averaged AN. The first of these values proved to be 1.1-1.6 (average 1.4) times greater than the second one, due to a sudden worsening of light conditions during the morning and evening hours. Because the value of the random error of AN determination frequently amounts to 30-40%, such a difference should be regarded as insignificant. From this it follows that the maximum AN values in a water column, measured during exposure of samples to natural light for half or all of the daylight period, can be roughly regarded as obtained under optimal light conditions.

Some authors [Rodhe et al., 1958; Sushchenya, Finenko, 1965; Finenko, 1967] regard the assimilation number obtained at depths of maximum photosynthesis during in situ experiments as a value characteristic of optimal light conditions in a water column. In this case, it would be more correct to regard the maximum AN in a water column as such, inasmuch as its position sometimes does not coincide with the position of the maximum values of production due to the irregular vertical distribution of chlorophyll [Holmes et al., 1957; Holmes, 1958; Forsbergh, 1963; Wauthy, Le Bourhis, 1968; Sokolova, Solov'yova, 1971]. In such cases, the AN values at depths of maximum photosynthesis are 10-40% smaller than the maximum assimilation numbers in the water column.

RESULTS OF AN MEASUREMENTS IN CULTURES AND NATURAL POPULATIONS OF MARINE PHYTOPLANKTON

In order to establish the variation range of AN under optimal or near-optimal light conditions, we must briefly review the results of AN measurements carried out by different researchers. The AN values for cultures of unicellular algae are given in table 1, and those for natural populations of marine phytoplankton in table 2 (under conditions of continuous artificial illumination) and table 3 (in natural light).

The tables indicate which method was used to measure photosynthesis, the radiocarbon method without correction for respiration (^{14}C), the radiocarbon method with correction for respiration for the calculation of actual photosynthesis ($^{14}C_{act}$), or the oxygen method (O_2act). A large portion of the AN determinations in natural populations is based on the use of the first method, while AN determinations in cultures are based on the second and third methods. It should be said that with the optimal photosynthetic light intensities, the intensity of respiration (R) constitutes only about 10% of the intensity of actual photosynthesis (P) in cultures of plantonic algae and in natural phytoplankton populations which do not lack biogenic elements. This low R/P ratio results in the absence of reliable differences between the actual and observable photosynthesis [Thomas, 1962]. (95)

Almost all the authors listed in tables 1, 2 and 3 determined the content of chlorophyll "a" by means of the spectrophotometric method, the calculations being carried out either by the formulas of Parsons and Strickland [1966] and SCOR-UNESCO [1966], or by Richards and Thompson's formula [1952] which gives

us results that are 1.33 times too high. In the second case, this value was used as a correction factor prior to the tabulation of the AN values.

The AN values given in the tables were calculated by us on the basis of simultaneous determinations of the chlorophyll "a" content and the intensity of photosynthesis, or were taken directly from other references.

Table 1 gives the results of AN measurements in vigorous cultures of various planktonic algae with a sufficient supply of biogenic elements. The AN variation range for cultures grown under the conditions of moderate and intensive illumination ($\geqslant$3000 lux) is 1.0-21.0 mgC/mg chl. "a" per hr. As we can see, the AN values for some species of algae were higher with a higher temperature and more intensive light during cultivation.

The AN variation range for marine phytoplankton, measured under the conditions of continuous (see table 2) and natural illumination (table 3), proved to be approximately the same, constituting 0.1-57.5 mg C/mg chl. "a" per hr, though these values usually lie within the limits of 0.5 and 15.0 mg C/mg chl."a" per hr.

AN values higher than 40 mg C/mg chl. "a" per hr were obtained in only two cases [table 2: Ryther, Yentsch, 1958; table 3: Forsbergh, 1963], and are probably an artifact. We have more reason to regard 35 mg C/mg chl. "a" per hr as the upper limit of AN. The rate of division of the algae, calculated on the basis of this value, is not at variance with the literature.

Table 1

AN values (mg C/mg chl. "a" per hr) during exposure to light, for cultures of various algae with a sufficient supply of biogenic elements

Algae	Light conditions during cultivation	Temp. during cultivation and AN measurement, C	Method of measuring photosynthesis	A N	Reference
Green peridinean and diatom algae	–	–	O_2act	4.2–12.7	Ryther, 1956
Diatom, peridinian, green and yellow-green algae	11,000 lux	15	"	6.4*	Ryther,
	11,000 lux	10	"	3.7*	Yentsch, 1957
Chaetoceros affinis	5,400 lux	14–16	"	11.6–12.8	Talling, 1960
Chlorella vulgaris	3,000 lux	21	$^{14}C_{act}$	2.0	Steemann,
	30,000 lux	21	"	6.8	Nielsen, 1961
Cyclotella meneghiniana	3,000 lux	21	"	2.1–3.4	Jorgensen, 1964
	30,000 lux	21	"	3.6–4.4	
Dunaliella tertiolecta	0.15 Cal/cm^2·min	25	O_2act	7.1	McAllister et
	0.05 Cal/cm^2·min	25	"	4.9	al., 1964
Skeletonema costatum	0.05 Cal/cm^2·min	25	"	6.2	
Monochrysis lutheri	0.05 Cal/cm^2·min	25	"	4.7	
Coccolithus huxleyi	5,400 lux	14–16	^{14}C	0.8–3.4	Jeffrey, Allen,
Hymenomonas sp.	5,400 lux	14–16	"	0.9–2.2	1964
Nannochloris atomus	10,000 lux	5	"	1.1	Yentsch, Lee,
	10,000 lux	10	"	3.3	1966
	10,000 lux	20	"	4.5	
	6,000 lux	20	"	1.5	
	2,000 lux	20	"	0.5	
Chlorella pyrenoidosa	3,000 lux	20	$^{14}C_{act}$	3.6	Steemann, Nielsen,
	21,000 lux	20	"	10.0	Jorgensen, 1968
Skeletonema costatum	3,000 lux	2	"	2.8	
	3,000 lux	8	"	4.0	
	3,000 lux	20	"	4.5	
Skeletonema costatum	3,000 lux	20	"	5.1	Jorgensen, 1969
	30,000 lux	20	"	9.2	
Cyclotella meneghiniana	3,000 lux	20	"	4.8	
	30,000 lux	20	"	6.6	
Nitzschia palea	3,000 lux	20	"	2.2	
	30,000 lux	20	"	4.0	
Nitzschia closterium	3,000 lux	20	"	2.4	
	30,000 lux	20	"	3.2	
Scenedesmus quadricauda	3,000 lux	20	"	2.9	
	30,000 lux	20	"	4.6	
Scenedesmus obliquus	3,000 lux	20	"	3.1	
	30,000 lux	20	"	3.8	
Ankistrodesmus falcatus	3,000 lux	20	"	2.1	
	30,000 lux	20	"	3.2	
Chlamydomonas moewusii	3,000 lux	20	"	2.4	
	30,000 lux	20	"	3.3	
Monodus subterraneus	3,000 lux	20	"	3.4	
	30,000 lux	20	"	3.4	
Synechococcus elongatus	3,000 lux	20	"	5.6	
	30,000 lux	20	"	8.3	
Chaetoceros gracilis	0.05 Cal/cm^2·min	21	^{14}C	3.4–7.6	Thomas, Dodson, 1972

(table 1 continued)

Algae	Light conditions during cultivation	Temp. during cultivation and AN measurement, C	Method of measuring photosynthesis	A N	Reference
Ditylum brightwellii	0.03 Cal/cm^2·min	20	O_2act	8.0	Berseneva et al., 1978
	0.16 Cal/cm^2·min	20	"	15.0	
Chaetoceros curvisetus	0.03 Cal/cm^2·min	20	"	18.0	
	0.16 Cal/cm^2·min	20	"	20.0	
	0.40 Cal/cm^2·min	20	"	21.0	
Chaetoceros socialis	0.03 Cal/cm^2·min	20	"	6.0	
	0.16 Cal/cm^2·min	20	"	11.0	
Peridinum trochoideum	0.03 Cal/cm^2·min	20	"	6.0	
	0.16 Cal/cm^2·min	20	"	7.0	
Gymnodinium kovalevskii	0.03 Cal/cm^2·min	20	"	11.0	
	0.16 Cal/cm^2·min	20	"	14.0	
Gyrodinium fissum	0.03 Cal/cm^2·min	20	"	2.5	
	0.40 Cal/cm^2·min	20	"	4.0	
Scenedesmus quadricauda	0.03 Cal/cm^2·min	20	"	5.5	
	0.16 Cal/cm^2·min	20	"	7.5	

*arithmetical mean

The ratio of the carbon content to the chlorophyll "a" content in marine phytoplankters with a sufficient supply of nutrients is equal to 25 [Antia et al., 1963]. From this we can easily calculate that the P/B coefficient will be equal to 17 with a 12-hour day length and an AN equal to 35. Using the formula relating the rate of cell division to the P/B coefficient [Koblentz-Mishke, Vedernikov, 1973], we can show that such a high value of the P|B coefficient will correspond to approximately 4 cell divisions per day. According to Z.Z. Finenko and L.A. Lanskaya [1971], such a high rate of division is possible in small algae. These authors have shown that with optimal light conditions and an excess of biogenic elements, marine unicellular algae usually divide 1-4 times a day in cultures. (100)

Table 2

AN values (mgC/mg chl. "a" per hr) under conditions of continuous artificial illumination for natural populations of marine phytoplankton from the upper layers of the euphotic zone

Study area	Month	Intensity of light	Method of measurement	A N		References
				range	arithmetical mean	
E Pacific, 30°N., 9°S	X-XII	11,000 lux	^{14}C	0.2-15.7	6.0	Holmes et al., 1957
Coastal waters in the vicinity of Woods Hole	I-XII	21,000 lux	O_2act	–	7.6	Ryther, Yentsch, 1957
E Pacific, 5-20°N	X-XII	11,000 lux	^{14}C	0.9-9.9	3.7	Holmes, 1958
Coastal waters in the vicinity of New York	X-VII	16,000 lux	O_2act	1.1-33.3	7.2	Ryther, Yentsch, 1958
	XII-VII	16,000 lux	^{14}C	0.3-53.0	3.7	
18°20' N, 114°45' W	V	11,000 lux	^{14}C	2.0-5.8	3.9	Shimada, 1958
N Atlantic 58-65°N	VII	Light saturation	$^{14}C_{act}$	4.1-4.7	4.4	Steeman, Nielsen, Hansen, 1959
N Atlantic 51-52°N	VIII	Light saturation	"	5.4-5.6	5.5	
Tropical Atlantic 50°N, 145°W	VII-VIII	0.08 Cal/cm^2 · min	^{14}C	0.8-2.4	1.7	McAllister et al., 1960
85°N, 140°W	VII-VIII	21,500 lux	"	0.5-1.1	0.7	English, 1961
Baffin Bay, Davis Strait	VII	75% light saturation	$^{14}C_{act}$	0.4-3.6	1.8	Steemann, Nielsen, Hansen, 1961
Aberdeen Lake	I-XII	11,000 lux	^{14}C	1.2-2.2	1.5	Steele, Baird, 1961
Fladens* Ground	I-XII	11,000 lux	"	0.9-2.1	1.5	
Long Island, estuary	VII-VIII	16,000 lux	O_2act	0.7-5.0	3.3	Lorenzen, 1963
50°N, 145°W	VII	0.07 Cal/cm^2 · min	^{14}C	1.5-3.5	2.7	McAllister, 1963
43-48°N, 124-127°W	I-XII	9,200 lux	"	2.2-12.9	4.7	Anderson, 1964
Sargasso Sea 32°N, 65°W	XI	16,000 lux	"	0.2-3.4	1.4	Goering et al., 1964
Japanese Inland Sea	I-XII	12,000 lux	"	1.0-20.0	6.0	Hirota, Endo, 1964
Various bays of Japan	I-XII	10,000-13,000 lux	"	0.6-32.3	5.6	Matsudaira, 1964
50-64°S, 16°W-86°E	XII-I	10,000 lux	"	1.0-2.7	1.6	Saijo, Kawaschima, 1964
Weddell Sea; Drake Passage	XII-I	32,000 lux	"	1.4-4.8	2.7	El-Sayed, Mandelli, 1965
W Tropical Pacific; Tasman and Coral seas	I-III	12,000 lux	"	1.4-5.3	–	Jitts, 1965
Coastal waters of the Antarctic Peninsula	II-III	50,000 lux	"	0.4-3.5	–	Mandell, Burkholder, 1966
Tropical Atlantic	XI	10,000 lux	"	3.0-4.0	3.5	Yentsch, Lee, 1966
Coastal waters of Puerto Rico	II-VII	51,000 lux	"	2.0-13.0	6.9	Burkholder et al., 1967
Pacific Ocean						Burkholder,
60-67°S	V-XII	22,600 lux	"	–	1.0	Burkholder, 1967
50-60°S	V-XII	22,600 lux	"	–	1.5	
40-50°S	V-XII	22,600 lux	"	–	2.9	
Drake Passage	III-XI	0.16 Cal/cm^2 · min	"	1.0-5.2	3.0	Mandelli, 1967
Mozambique Channel	VII-XI	10,000 lux	"	3.2-8.2	6.0	Sournia, 1967

*conjectural spelling – transl.

(table 2 continued)

Study area	Month	Intensity of light	Method of measurement	AN range	AN arithmetical mean	References
Coastal waters of Long Island	I–XII	Light saturation	^{14}C	0.8–9.3	4.3	Mandelli et al., 1970
5°N–20°S, 105–112°W	II–IV	0.09 Cal/cm^2·min	"	1.2–6.2	4.1	Thomas, 1970
E Tropical Pacific	V–XII	0.06 Cal/cm^2·min	"	0.7–21.0	6.5	Malone, 1971a
Caribbean Sea	V	0.06 Cal/cm^2·min	"	3.1–10.3	5.9	
25–44°N, 150°E	VI	20,000–30,000 lux	"	1.7–6.7	4.4	Takanashi, Ichimura, 1972
50°N–15°S, 155°W	VIII–X	10,000–15,000 lux	"	1.1–5.2	2.4	Takanashi et al., 1972

The extensive range of AN fluctuations in natural marine populations (tables 2, 3) in comparison with cultures (table 1) is obviously due to the fact that the habitats of algae are more diverse in nature than in cultures. The maximum AN values are observed in the abundant coastal waters of middle and low latitudes, while the minimum values are characteristic of the high latitudes and the subropical and tropical areas with the least phytoplankton. These peculiarities of AN distribution in marine phytoplankton are due to the fact that this index is related to temperature, the trophic state of the waters, and to the conditions of mineral nutrition of the algae [Vedernikov, 1975, 1976].

In fresh waters, the AN fluctuation range under optimal illumination conditions is similar to that in cultures, and constitutes 0.1–11.5 mgC/mg chl. "a" per hr [Manning, Juday, 1941; Gessner, 1949; Rodhe et al., 1958; Wright, 1959, 1960; Vinberg, 1960; Ivanova, 1961; Saijo, Sakamoto, 1964; Pyrina, 1967; Kuz'micheva, 1970; Kovalevskaya, 1979].

Thus, the most common AN values for planktonic algae in cultures and natural marine and freshwater populations under optimal illumination conditions lie within the range of 0.5–15.0 mgC/mg chl. "a" per hr.

Table 3

AN values (mgC/mg chl. "a" per hr) in optimal natural light for natural populations of marine phytoplankton from the upper layers of the euphotic zone

Study area	Month	Method of measuring photosynthesis	A N		Reference
			range	arithmetical mean	
E Pacific 10°N–5°S	X–XI	^{14}C	0.1–16.0	8.4	Holmes et al., 1957
E Pacific 8–24°N	XI–XII	"	1.3–10.6	5.4	Holmes, 1958
Coastal waters of Brazil 25°07 S, 47°51 W	VII	O_2act	12.9–15.7	14.3	Garcia Occhipinti et al., 1961
Florida Current 25°33'N, 79°25'W	IV–VIII	^{14}C	0.2–0.8	0.5	Corcoran, Alexander, 1963
Gulf of Panama 8°40' N, 79°20' W	I–XII	"	4.1–57.5	16.7	Forsbergh, 1963
Hakodata Bay 44°45' N, 140°40' E	III	"	–	2.4	Motoda et al., 1963
1°–16°S, 16–37° W	IX–X	"	–	10.8	Sushchenya, Finenko, 1965
Black Sea 43°N, 29–38°E	VIII–IX	"	3.3–9.1	6.7	Finenko, 1965
Sevastopol Bay	IV–XII, I	"	1.5–15.6	5.1	
Sea of Azov	VI	"	2.5–14.8	6.6	
Coastal waters of Oregon	I–XII	"	6.0–16.7	11.5	Curl, Small, 1965
44°40' N, 124°40' W	3/VI	"	22.6	–	
	19/VII	"	28.0	–	
0°0' 145°W–160°E	II–III	"	–	2.0	Wauthy, Le Bourhis, 1966
Beaufort Strait 34°40'N, 76°35' W	I–XII	O_2act	2.5–26.4	10.6	Williams, Murdoch, 1966
Coastal waters of NW Madagascar	I–XII	^{14}C	–	12.0	Angot, 1968
Coastal waters of NW Madagascar	I–XII	"	3.9–12.6	9.1	Sournia, 1968
14–43°N, 15–25°W	VI–VII	"	0.5–4.4	2.6	Wauthy, Le Bourhis, 1968
45°10'N, 126°56' W	26/VII	"	2.9	–	Anderson, 1969
Coastal waters of South Orkney Islands	I–III	"	0.6–1.1	0.8	Horne et al., 1969
Coastal waters of Peru 13–17°S	III	"	1.7–7.4	4.8	Strickland et al., 1969
44–46°N, 153–157°E	VII–IX	"	3.5–16.0	8.8	Koblents-Mishke et al., 1970
Black Sea	VIII–IX	"	5.0–7.0	6.0	Finenko, 1970
Red Sea	X–XI	"	–	5.0	Khmeleva, 1970
Gulf of Aden	XI	"	–	12.0	
Coastal branch of Peru Current 8–23°S	IX–XI	"	8.0–26.2	17.8	Vedernikov, Starodubtsev, 1971
Oceanic branch of Peru Current; Peru counter-current 5–30°S	IX–X	"	5.6–8.1	7.4	

(table 3 continued)

Study area	Month	Method of measuring photosynthesis	AN		Reference
			range	arithmetical mean	
Dal'nezelenetskaya Bay 69°07'N, 36°05'E	V-X	^{14}C	0.4-6.7	2.1	Sokolova, Solov'-yova, 1971
Hawaiian Islands; Kaneohe Bay	III-VI	"	11.5-13.0	12.0	Capeton et al., 1971
Fanning Is. lagoon	9/I	"	20.6	-	Gordon et al., 1971
Coastal waters of Nova Scotia	1/VI	"	3.4	-	Platt, Conover, 1971
Coastal waters of East and West Murman	VI-VIII	"	0.1-2.3	1.2	Vedernikov, Solov'-yova, 1972
Coastal waters of Nova Scotia	VIII	"	0.4-3.2	1.3	Chung Li Choi, 1972
Gulf of Alaska and Aleutian Trough	III-V	"	2.9-12.8	5.9	Kovalevskaya, Giginyak, 1973
4°N-10°S, 155-172°E	XII-II	"	0.7-2.4	1.3	Koblentz-Mishke (unpublished data)
Antarctica 55-57°S, 25-50°W	XI-XII	"	0.6-0.9	0.7	Kabanova et al., 1974
Subantarctica 45°15'S, 56°39'W	20/XII	"	1.0	-	
Subtropics and tropics 0-45°S, 19-54°W	XII-I	"	0.7-3.8	2.2	
Equator 97-154°W	I-II	"	1.6-5.3	3.0	Vedernikov et al., 1975
Coastal waters of Peru	II-III	"	5.4-17.3	7.8	

It is interesting to compare the AN for unicellular algae with those of multicellular algae and phanerogams. The AN for multicellular freshwater algae (Chara, Mougeotia, Spirogira) were found to be equal to 0.8-2.4 mgC/mg chl. "a" per hr [Hammann, 1957].

(102)

With saturation concentrations of CO_2 and a temperature of 20°C, the AN vary from 1.4 to 3.9 mgC/mg chl. "a" per hr for the green leaves of higher terrestrial plants, and from 15.0 to 32.6 mgC/mg chl. "a" per hr for yellow leaves [Rabinovich, 1953, p. 417]. In Rabinovich's opinion, such high values for the yellow leaves are due to the fact that the abnormally low content of chlorophyll in them is not accompanied by a proportional decrease in the enzyme which limits the rate of photosynthesis.

Abnormally low AN (approximately 0.3 mgC/mg chl. "a" per hr) were obtained by Hammann [1957] for a large number of submersed phanerogams. Enrichment of the water with carbon dioxide increased the AN only 1.5-fold in the majority of species studied. Westlake [1975] gives higher AN (1-2.5 mgC/mg total chl. per hr) for floating phanerogams.

From this it follows that under optimal illumination conditions, the AN values lie within the range of 0.1-35.0 mgC/mg chl. "a" per hr in unicellular algae and terrestrial phanerogams, and they do not usually exceed 3.0 mgC/mg chl. "a" per hr in multicellular algae and aquatic phanerogams.

(103)

AN VALUES IN DIFFERENT SIZE AND TAXONOMIC GROUPS OF MARINE PLANKTONIC ALGAE

Hammann [1957] was involved in studying the biotic factors which determine the assimilation number in plants. He succeeded in showing that the AN depended on the development of the upper surface which is effective in CO_2 uptake. The author established a significant decrease in assimilation with an increase in the closely superjacent layers of Chlorella cells obtained by filtration.

The assimilation value of closely superjacent strips cut from a leaf of Nuphar luteum constitutes 35% of the assimilation value of the same strips placed next to each other. Comparative experiments with the outer strip, which was first killed in boiling water, showed that the decrease in assimilation with a decrease in surface is determined mainly by the resistance of the tissues, which prevents the permeation of CO_2 to the chloroplasts.

The author comes to the conclusion that the AN values decrease parallelly with the effective surface in unicellular algae and submersed phanerogams.

It is known that phytoplankters vary drastically in size and chlorophyll content. Naturally, different-sized cells have a different specific surface (S/V). In the Gulf of Panama, for example, the specific surface varies from 3.14 to 0.01 $\mu m^2/\mu m^3$ with diatom cells varying from 51 to 11,740,000 μm^3. As we know, many of the planktonic diatoms, which constitute the greater part of the phytoplankton biomass in the majority of the oceans [Cushing, 1955], have a vacuole. The chromatophores are found in the thin layer of plasma which lies next to the inner walls of the valves, and so the surface/plasma ratio (S/P), rather than the specific surface, may be the really important factor in supplying the chromatophores with CO_2. Due to the fact that the relative size of the vacuole increases as the size of the diatom cells increases [Jorgensen, 1964; Smayda, 1965], the fluctuations in cell size have a smaller effect on the S/P ratio, than on the S/V ratio. According to Smayda's calculations [Smayda, 1965], the S/V ratio in Skeletonema costatum f. tropicum (V=1000 μm^3) was 3.7 times greater, and S/P 2.3 times greater than in Guinardia flaccida (V=78,400 μm^3). The different ratio of plasma volume to cell volume in small and large diatoms results in a situation where the content of chlorophyll per unit of cell volume increases as the cell diminishes [Yentsch, Ryther, 1959a; Jorgensen, 1964], which also should reduce the effect of the change in cell size on the supply of CO_2 to the chloroplasts.

Due to the fact that the ratio of cell surface to plasma volume and to the chlorophyll content in small and large cells is nevertheless different, we should examine the possibility of the assimilation number being affected by the size of the cells and the content of chlorophyll in them. Jorgensen [1964] showed that a 2.2-fold change in the chlorophyll content of the cells per unit volume did not affect the value of the assimilation number in cultures of Cyclotella meneghiniana. The photosynthesis/chlorophyll ratio in Chlorella cells remained constant, though the content of chlorophyll per unit of cell volume varied more than 10-fold due to changes in the concentrations of Fe and N in the culture [Fleischer, 1935]. A deficiency of Mg in these cultures reduced the assimilation number as a result of its direct effect on the process of photosynthesis. In Smayda's experiments [1965] carried out in the Gulf of Panama at a depth of 10 m, no clear relationship was detected between the 10,000-fold fluctuations in the content of chlorophyll per unit of diatom plasma and the values of the daytime assimilation number. Consequently, on the basis of the data available to us, we can conclude that even fairly extensive changes in the chlorophyll content of the cells do not have any direct effect on the value of the assimilation number. (104)

A similar conclusion is reached during 2—3-fold cell-volume changes in diatom cultures [Jorgensen, 1964]. On the other hand, more drastic fluctuations in cell size can affect the assimilative activity of the chlorophyll. Malone [1971 a, b] compared the AN for net plankton and nannoplankton. He separated them by filtering the samples of seawater through milling gauze

with a 22 μ mesh. The mean AN for these two fractions of phytoplankton in the Caribbean Sea and in the eastern tropical Pacific between 0 and 25° N did not differ significantly. On the other hand, the AN in the nannoplankton of the California and Peru currents proved to be twice as high as in the net plankton. Saijo and Takesue [1965] obtained similar results in the Indian Ocean when they compared the AN of all the phytoplankton (>0.45 μ) with the AN of the net plankton (>90 μ). In the upper layers of the euphotic zone, the first of these values were on the average 2.7 times higher than the second ones. The AN for phytoplankton entrapped with microporous filters with different-sized pores (0.45, 0.8, 5 μ) did not differ from each other. The results of these and Malone's experiments show that the assimilative activity of chlorophyll in large phytoplankters entrapped with milling gauze with a mesh size of several tens of microns may be 2-3 times lower than in smaller phytoplankton. The high assimilation numbers in the nannoplankton may be due to both the good CO_2 supply to the chloroplasts, and to the high level of metabolism in small cells. The second assumption is based on the fact that an inverse relationship between the rate of cell division and cell volume is observed in phytoplankters [Finenko, Lanskaya, 1971].

Nannoplankton predominates in various regions of the World Ocean, at least at the lower and middle latitudes [Yentsch, Ryther, 1959a; McAllister et al., 1960; Gilmartin, 1964; Subrahmanyan, Sarma, 1965; Semina, 1969; Malone, 1971 a, b]. O.I. Koblents-Mishke and V.I. Vedernikov [1973] have shown that cells with a volume of 10^4-10^5 μ^3 constitute the highest percentage

of the biomass in ocean waters varying in trophic state. From this we can conclude that the effect of the size composition on the assimilation number in natural populations of marine phytoplankton is of secondary significance.

In addition to size composition, the metabolic differences in various species or taxonomic groups could be the biotic factors that determine the value of AN. This question is best studied with cultures of algae in which the factors affecting the value of AN are more or less the same. The illumination conditions to which the algae are adapted, temperature and the conditions of mineral nutrition should be included among the main abiotic factors that determine the assimilation number during light saturation. Furthermore, the assimilation number varies during the different developmental stages of the cultures. In Jeffrey and Allen's experiments [1964], the assimilation number during the stage of logarithmic growth in chrysomonad cultures increased from 0.8-0.9 to 2-3, reaching the maximum value at the end of this stage. Later, during the stationary stage, the AN diminished to 0.7-0.8 in 28-day cultures. All the AN values given in table 1 apply to vigorous cultures with an excess of biogenic elements, but since the authors did not indicate the exact stage of culture growth, the disconnectedness of the AN values in table 1 can be partly attributed to the differences in the physiological activity of the cells. The same can be achieved by using the constant assimilation coefficient (AC) 1.25 for converting oxygen to carbon without taking into account the elementary composition of the algae and the source of nitrogen nutrition, the changes in which affect the AN [Vinberg, 1960, p.59].

Taking all the above data into account, we shall attempt to compare the assimilation number in different species and in different taxonomic groups. It is very convenient to use for this purpose the results of the investigations carried out with freshwater and marine algae in Steemann Nielsen's laboratory with the help of the radiocarbon method at 20°C [table 1: Steemann Nielsen, 1961; Jorgensen, 1964, 1969; Steemann Nielsen, Jorgensen, 1968]. The algae used in these investigations belong to four types, i.e. diatoms (Cyclotella meneghiniana, Nitzschia closterium, N. palea, Skeletonema costatum); Chlorophyta (Ankistrodesmus falcatus, Chlamydomonas moewusii, Chlorella pyrenoidosa, C. vulgaris, Scenedesmus obliquus, S. quadricauda); Heterocontae (Monodus subterraneus), and Cyanophyta (Synechococcus elongatus). The assimilation numbers for cells adapted to 30,000 lux were equal to 5.8 ± 2.7 in diatoms, 5.3 ± 2.6 in green algae, 3.4 in M. subterraneus and 8.3 in S. elongatus. For cells adapted to 3,000 lux, these values amounted to 3.6 ± 1.5, 2.7 ± 0.6, 3.4 and 5.6 respectively. The difference between the mean values in the green algae and diatoms proved to be insignificant both for shaded and illuminated cells. The assimilation numbers in the other two types, with the exception of 5.6, lay within the limits of the mean square deviation from the mean AN value for diatoms. It should be said that 3-fold changes in AN were observed between species belonging to the same type in illuminated cells, and 1.5-2-fold changes in shaded cells. It is quite possible that these fluctuations were due to changes in the physiological activity of the cells taken from cultures at different stages of logarithmic growth, rather than to species differences. If the assimilation

number really does depend on species composition, then we can assume that the differences in chlorophyll activity are greater in different genera, than in species of the same genus. For instance, the AN values for illuminated cells in different members of the same genus and the maximum deviations from them amounted to 4.2 ± 0.4 for Scenedesmus, 8.4 ± 1.6 for Chlorella and 3.6 ± 0.4 for Nitzschia.

Some authors have obtained results similar to the ones presented above (see table 1). In the experiments of McAllister and coauthors [McAllister et al., 1964], the assimilation numbers in three cultures of Chlorophyta, diatoms and Chrysophyta grown under illumination conditions of 0.05 Cal/cm^2·min differed insignificantly, and constituted 4.9, 6.2 and 4.7 respectively. In Ryther and Yentch's experiments [1957] with cultures of diatoms, Chlorophyta, Chrysophyta and peridinians, the AN variation coefficient constituted only 17%. Ryther [1956] simultaneously measured the content of chlorophyll and the intensity of photosynthesis under continuous illumination for 14 cultures of various phytoplankters belonging to different types. Having obtained a linear relationship between the intensity of photosynthesis and the content of chlorophyll, the author came to the conclusion that the species composition of the phytoplankters did not affect the value of the assimilation number.

In the investigations carried out recently by Berseneva et al. [1978] (see table 1), the assimilative activity of diatoms (11-21 mgC/mg chl. "a" per hr) grown under the conditions of high light intensity proved to be higher than in peridinians (4-14 mg C/mg chl. "a" per hr) grown under the same conditions. Such a

difference can be partially attributed to the differences in the size of the species studied from these two groups of algae.

On the basis of most of the above results of experiments with cultures, we can conclude that different taxonomic groups of phytoplankters have the same mean AN. It would be very interesting to establish whether this also holds true for natural populations of phytoplankton. This is a difficult undertaking, as it is impossible to determine the age of the populations under study, and the conditions prior to the experiment. From this we can conclude that the results of investigations with natural populations are less conclusive than those conducted with cultures, but they can provide us with additional information if an abundance of data is collected. (106)

In a number of investigations with natural phytoplankton populations, the species composition was found to have no effect on the value of the assimilation number. In experiments carried out in cement reservoirs with natural marine populations enriched with biogenic elements, Edmondson [1955] observed a close relationship ($r=+0.81$) between the chlorophyll content of the water and the intensity of photosynthesis, related to a unit of surface irradiance. The ratio between these values was approximately the same in populations consisting mainly of diatoms, and in populations with a predominance of peridinians and green algae. In the northern part of the Pacific Ocean (42-61°N), Motoda and Kawamura [1963] did not find that the value of the assimilation number was affected by the replacement of certain dominant diatoms by others. In a number of investigations, no differences

were observed in the assimilative activity of chlorophyll between diatoms and blue-green algae. In the coastal waters of Madagascar, the AN values in populations with a predominance of diatoms did not differ from the AN obtained for populations with a predominance of blue-green algae [Sournia, 1968]. Ichimura and Aruga [1958] have studied the relationship between photosynthesis and temperature during different months in the natural populations of eutrophic lakes, which consisted of diatoms and blue-green algae. The AN values under temperatures most favourable to each group (15° for diatoms and 22-25° for blue-green algae) proved to be identical. According to Pyrina's data [1967], the daytime assimilation numbers in the surface layer of reservoirs during the summer period are approximately the same in diatoms, blue-green algae and in mixed populations.

Some papers present data on the differences in the photosynthetic activity of diatoms and peridinians. Hirota and Endo [1964] attributed the sharp increase in the assimilation number at two stations in the Inland Sea to the intensive development at these stations of Gonyaulax polygramma. However, at two other stations which were also distinguished by the development of peridinians (Prorocentrum micans and Ceratium fusus), no increase in assimilation number was observed in comparison with neighbouring stations at which diatoms predominated. During Mandelli's year-long investigations of neritic phytoplankton populations off the coast of Long Island [Mandelli et al., 1970], the assimilation numbers under the conditions of light saturation and a temperature of 10-20°C were equal to 2-4 mgC/mg chl. "a" per hr

when diatoms prevailed, and 5-9 mgC/mg chl. "a" per hr when peridinians predominated. Since peridinians predominated from April to August, and diatoms the rest of the year, it is possible that the high AN during the predominance of the peridinians were due to seasonal changes of AN, which were caused by other abiotic factors besides temperature. According to the data of Taniguchi [1969] and Kawamura [1963], the assimilative activity of chlorophyll in Bering Sea populations with a predominance of peridinians proved to be several times higher than in populations where diatoms predominated. We cannot reach any final conclusion regarding AN differences in the diatoms and peridinians of the Bering Sea on the basis of these studies, as the authors did not compare the abiotic factors of the environment for the different stations.

Contrary to the above results of the Japanese researchers and Mandelli et al., Hagmeier [1967], on the basis of his investigations in Helgoland waters, came to the conclusion that the photosynthetic activity (P/B coefficient) of diatoms is 4 times higher than in peridinians.

(107)

On the basis of the above review of investigations with cultures and natural populations of phytoplankters in which the relationship between the assimilation number and the species composition of the algae was studied, it can be said that the assimilation numbers in diatoms and green algae, just as in diatoms and blue-green algae, do not differ significantly. Consequently, these types of algae have approximately the same assimilative activity of chlorophyll under illumination conditions most suitable for photosynthesis. A comparison of the photo-

synthetic activity in diatoms and peridinians, which was carried out by various authors, produced inconsistent results.

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ASSIMILATION NUMBER AND ITS VARIATION IN THE CULTURES AND NATURAL POPULATIONS OF MARINE PHYTOPLANKTON

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Summary

Summary tables of assimilation number were compiled on the basis of literary data. Measurements of this index were carried out in natural populations of marine phytoplankton and in cultures of plankton algae at optimum light intensity. Values of AN in cultures of different algae lie in the range from 1 to 21 mg C/mg chl. «a»·hour. Values of AN in natural populations of phytoplankton fall in the broad range between 0,1 and 35,0 mg C/mg chl. «a»·hour, although usually its values equall 0,5—15,0 mg C/mg chl. «a»·hour. Maximum values of AN were measured in coastal waters of temperate and low latitudes; minimum values of this index are characteristic of high latitudes and of oligotrophic tropical and subtropical waters of the World Ocean. The methods of AN determination and its dependency on species and size structure of phytoplankton are discussed.